

EFFECTS OF SOCIAL STRUCTURE ON THE FEEDING BEHAVIOR AND SPATIAL DISTRIBUTION OF *ALOUATTA PALLIATA*

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Abstract: Interactions between animals living in groups may have important implications for individuals within the group. We hypothesized that the dominance relations between males and females within groups of howler monkeys, *Alouatta palliata*, may affect the amount of time spent feeding as well as the spatial distribution of resting individuals. To test these hypotheses, we recorded behaviors (resting, feeding, traveling, observing, and interacting) of individuals in three groups of howlers over two days. Females spent a significantly greater proportion of time feeding than males, but the sexes did not differ in other recorded activities. There was no obvious trend between sex and spatial distribution during rest periods. The difference in foraging time between sexes may have been due to males displacing females from the highest quality feeding places or foods. Alternatively, females may have had higher energetic demands and needed to consume more food than males. Although intersexual competition occurs within groups, females may accrue compensatory benefits from group living due to increased access to food resources or increased vigilance of group members.

Key Words: dominance, food competition, howler monkey, rank

INTRODUCTION

In groups that are stratified by dominance rank, social interactions may be an important determinant of group dynamics. Howler monkeys (*Alouatta palliata*) form social groups consisting of adult males, adult females, and juveniles (Glander 1983). Within each sex there is a dominance hierarchy, but all adult males are dominant over all females (Glander 1983). As subordinate members of the group, females may be displaced from high quality food sources by adult males. To compensate for this, females may need to consume more food to meet their daily nutritional requirements (Robinson 1981) or may need to travel more to obtain sufficient quantities of food. We hypothesized that the dominance hierarchy between the sexes of howler monkeys affects activity budgets and predicted specifically that females, because of their subordinate rank, would spend a greater proportion of their time feeding than males.

Theory also suggests that central positions in a group are favored over edge positions due to decreased predation risk (Hall and Fedigan 1997). Males may therefore take advantage of their dominant rank to acquire the preferred central positions. We hypothesized that the social structure of howler monkeys affects the spatial positioning of the group during rest and predicted that during extended rest periods adult males would occupy central positions while females would be found on the periphery of the group.

METHODS

This study examined three howler monkey groups in the Palo Verde National Park on 10 - 11 January 2000. All data were collected between 07:15 - 11:30. We selected groups based on calling cues at dawn and proximity to the OTS Field Station. We observed one large group of approximately 30 monkeys on two mornings and two smaller

groups of 4 and 5 monkeys for one morning each.

We recorded the behavior of focal individuals from two dominance ranks, male and female (excluding females with infants) in each group. Each individual was monitored for at least 1 h that included one period of activity and one period of rest. The behavior or activity of each focal individual was recorded at 5 min time intervals throughout the observation period. We followed 10 females and 5 males and obtained 22.1 ± 4.7 observations per female and 31.6 ± 15.1 observations per male (means \pm SD). We classified behavior as: resting (sitting or lying without any other activity), feeding (searching for or manipulating food), traveling (walking or climbing not accompanied by any other activity), observing (stationary with alert posture or demeanor, including calling), and interacting (engaging in prolonged contact with another individual, excluding resting). For each individual we calculated the percentage of observations allocated to each activity within the monitoring period and then averaged these for each sex. Percentage of observations was considered equivalent to percentage of time spent in each activity. Mean percentage of time spent in each activity category was compared between the sexes with Student's t-tests.

During two resting periods of one group in one morning, we described individual position by mapping the estimated lo-

cation of individuals on a 2-dimensional plane. Twenty-one individuals were mapped during the first resting period and 10 during the second, after the group split into two subgroups. To differentiate between central and edge positions, we calculated the diameter of the smallest circle that encompassed the mapped group and divided that area into equal central and edge areas, using the following relationships: radius of inner circle = $(0.5r^2)^{1/2}$; areas = $(\pi r^2/2)$ where r = radius of the outer circle. Individuals were classified as occupying central or edge positions. We compared the ratio of center to edge resting positions for males and females using a G-test.

RESULTS

Focal females spent significantly more time feeding than focal males (Table 1). Males spent more time observing and traveling, while females spent more time resting and interacting, although these differences were not statistically significant (Table 1). On average, males also spent more time observing than females, but the variation among males was very high (range: 0 - 53%), and the difference between sexes was not significant (Table 1). Both males and females occupied central and edge positions in similar proportions (Fig. 1; 3:3 and 7:10, center:edge, for males and females, respectively; $G = 0.01$, $df = 1$, $p = 0.76$).

Table 1. Percentage of observation time allocated to five behaviors by male and female howler monkeys. Means \pm 1 SD. Mean number of observations per female individual (\pm 1 SD) = 22.1 ± 4.7 ($n = 10$). Mean number of observations per male individual (\pm 1 SD) = 31.6 ± 15.1 ($n = 5$).

Sex	% Feeding	% Resting	% Traveling	% Observing	% Interacting
Female	23.1 ± 6.7	60.3 ± 13.4	10.2 ± 6.2	5.1 ± 8.1	1.2 ± 2.0
Male	15.5 ± 11.4	52.2 ± 30.0	14.4 ± 4.5	17.9 ± 20.8	0.0 ± 0.0
t ^a	3.14	0.28	1.48	1.06	1.35
P	0.008	0.78	0.16	0.31	0.20

^a $df = 13$

DISCUSSION

As hypothesized, intersexual dominance patterns of howler monkeys were related to time spent on different activities, especially on feeding behavior. Dominant males spent less time feeding than did subordinate females. These results are consistent with other sex-dependent behavior patterns in primate species where dominant males occupy more advantageous foraging positions (Robinson 1981).

During the dry season in Costa Rica, energy-rich fruit and legume pods are relatively scarce and male howlers may exclude females from these resources (Stoner 1996). If females are forced to feed on leaves, a less nutritious food resource than fruit (Milton 1982), they would need to spend a greater proportion of time feeding to meet energy demands. However, we never observed a female being actively displaced from fruit by a male. Also, females did not travel more than males, or rest less, as might be expected if males were displacing them from better foraging locations.

An alternative explanation for why females might spend more time feeding than males is that females may have a higher metabolic demand than males. Robinson (1981) found that female wedge-capped capuchin monkeys (*Cebus nigrivittatus*) spent a greater proportion of their time actively consuming food than did males, but that the quality of food resources did not differ between the sexes. He proposed that this was due to differing energy demands between the sexes, a finding that may apply to male and female howler monkeys as well.

Our study indicated no difference in the spatial distribution of male and female howler monkeys during rest periods. However, our data were restricted to one group during two rest periods, so further observations are necessary to rigorously test this hy-

pothesis.

Finally, it is possible that even though intersexual competition occurs within groups, females accrue compensatory benefits from group living due to increased access to food resources or increased vigilance of group members. These possibilities illustrate both the difficulty of evaluating selection pressures at contemporary time scales and the importance of considering the tradeoff between the benefits and costs of individual behavioral traits.

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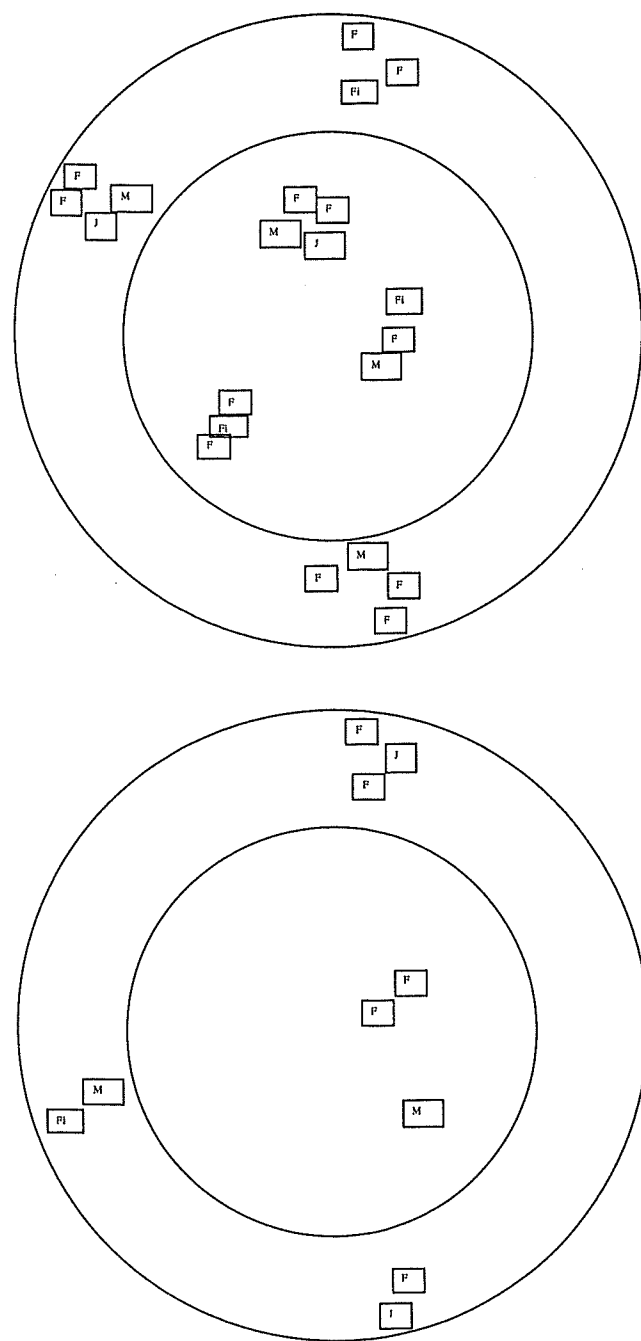


Figure 1. A two-dimensional spatial description of two resting positions for one group of howler monkeys, a) full group of 21 individuals and b) subgroup of 10 individuals, on 11 January 2000 at Palo Verde National Park. (F = Female, Fi = Female with infant, J = Juvenile, M = Male). Outer circle is the minimum area to encompass the entire group. Central positions were defined as those within the inner circle. Radii = 75 and 30 m for a and b respectively.